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The value of generic and specific characters tested by the wingmarkings of Sphingides

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Zoology. — *"The value of generic and specific characters, tested by the wingmarkings of Sphingides"*. By Prof. J. F. VAN BEMMELEN.

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Supposing the rules for the colour-pattern of the wings, which I deduced from former investigations by others as well as by myself — to be valid, they ought to prove fit as guides in the choice of a point of issue, when entering on the investigation of a new group, that is to say when searching for a form which shows the general pattern in its most original, least altered condition.

Judging by those rules, I believe that among Sphingides, as far as I am acquainted with them, *Smerinthus populi* is a very original form, in spite of the covering of red hairs, spread over the upper side of the rootfield of the hind-wings, there hiding the primitive pattern.

The arguments for this opinion are the far-going similarity of fore- and hind-wing, both on the upper and the underside, and the presence of a pattern, which over the entire wing-surface is built after the same simple motive, viz. regular alternation of darker and lighter transversal lines and bands, each composed of spots. In both the dark and the light bands the spots show a strong tendency to the semilunar shape (the convex side turned outward), but here and there they clearly approach the biconcave (hourglass) form. As to the shades occurring as well in the dark as in the light bands of spots, I pass them over for the present.

On the upper side of the fore-wing two of the darker lines run on both sides of the light discoïdal spot, and at a certain distance from it, thus separating a darker median field from two lighter transversal bands, which in their turn are again bordered by a similar ribbonlike series of dark spots. Across this dark central area, at the outside of the light discoïdal mark, another dark bar may be distinguished, and in the distal part of the area, between the last mentioned bar and the outer borderline, there also occurs a series of spots, which however are far fainter.

Moreover the anterior edge of the wing, on the inner side of the discoïdal spot, shows a lighter hue than the rest of the central area, which increases in darkness toward the posterior margin. In this

lighter part two small dark spots touching the front-rim of the wing may again be distinguished, each of them composed of two transverse striae. In some specimens of *Smerinthus populi* the proximal border-rim of the central area is also clearly double. Next to the wing-root in the lightgrey hue of this part, a faint indication of a dark ribbon may be detected besides.

Of the various hitherto mentioned bars of dark spots, the outermost, which is by far the strongest and completest, consisting of nine separate elements when accurately counted, takes a sinuous course. Counting from the front backwards, the fifth spot is situated furthest inward, it also is the shortest and straightest. In many specimens this spot is obviously darker in hue than the rest, and this difference deserves our attention, as it is met again in allied species, but here increased in intensity and extension.

On the inner and on the outer side of the just mentioned rows of spots there occurs a broader bar of less obscure and more faintly circumscribed markings, which however are evidently darker than the grey shade of the lightest wing-areas, playing the rôle of ground-colour. The outer of these two collateral bars is separated from the median series by a narrow sharply traced light interval. From the internal bar it differs by lesser regularity, some of its components being broader than the rest, and at the same time darker. This is especially the case with the spot near the hindborder of the wing, this spot broadening obliquely in an outward and posterior direction, and thereby just touching the hinder angle of the wing. A similar triangular broadening also occurs at the front end of the bar, near the apex of the wing, but here it has a lighter hue. I think it desirable to indicate these spots by special names, e. g. anterior and posterior triangular spot, as they are found again with increased clearness and independence in allied species.

In the middle part of the bar under discussion four of the spots clearly show the hourglass-type. In front of them the bar coalesces with a dark area, extending along the greater part of the outer margin of the fore-wing. This area forms a large convex blotch, occupying five internervural cells from the apex backward.

Though at first sight this blotch is not divided into separate spots, yet three darker centres may be distinguished in it, touching the foreside of the nervures which take their course through it. A comparison with other species of the same genus and of different allied genera again proves, that these darker centres may be considered as originally independent separate spots — one in each internervural cell — which have coalesced with each other into a single

almost homogeneous dark blotch. In front next to the apex, this blotch is sharply cut off from the above mentioned anterior triangular spot by an oblique light-hued line, the lastnamed spot moreover often showing a very light shade itself.

Now directing our attention especially to the points of correspondence between the various components of this wing-pattern, and on the contrary less heeding the differences, we are easily led to the conclusion that it is composed of seven transverse rows of dark spots, separated by lighter bars.

The external of these transverse rows (I) must then be looked for in the above-mentioned dark blotch along the external margin.

The second (II) is the complete row of nine spots, with its set of accompanying fainter bars.

The third (III) forms the external border of the dark central field.

The fourth (IV) is the dark line along the outer side of the discoidal mark, which although somewhat obliquely, may be said to run across the middle of the central area from fore- to hind-margin.

The fifth (V) is the inner front-line of the central field, this line being sometimes double.

The sixth (VI) the single, curved series of spots over the middle of the proximal light wing-area.

The seventh (VII) is formed by the faint traces of spots near the wing-root.

The light intervals between these seven bars may be indicated as in former publications by the letters A to G. In those intervals some traces of still other dark bars, varying in distinctness, are again met with; so it is not improbable that originally the stronger transverse bands everywhere alternated with less dark and sharply marked rows of spots.

In all these features the pattern of *populi* remarkably agrees with that of Arctiïds, as I described it in a former paper, and in the same way with that of numerous other families of Lepidoptera, as I hope to show afterwards [1]).

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[1]) Here I wish already to mention that Annette F. Braun, in a paper: Evolution of the Color Pattern in the Microlepidopterous genus Lithocolletis (Journal of the Academy of Nat. Sc. of Philadelphia XV 2d Ser. 1914) as the result of an ontogenetic and phylogenetic investigation about the colour-development on the forewings of these Tineids, gives as her opinion that all patterns of this polymorphic genus may be derived from seven dark transverse bars, forming to her mind a primary pattern, on which a secondary one, composed of still darker lines, will later on be so to say projected, as is also proved by the development inside the pupal sheath.

Moreover this pattern occurs almost completely on the hind-wing as well as on the front one. For also there the first row forms a convex dark blotch occupying five internervural cells along the outer margin, with three darker centres next to corresponding veins. In the same way the transverse bar II is composed of dark spots, curved outward and is accompanied on both sides by a less dark bar of more diluted spots. The number of components of bar II is smaller than on the fore-wing, the hinder three being concealed under the covering of red hairs. The fourth and fifth spot (counting from the front border) are straighter than the rest, and placed somewhat more inward, while they show rather a darker hue.

Row III and IV stand in contact with the corresponding ones of the fore-wing, but disappear under the red covering even sooner than II. V and VI are only indicated by dark spots along the front margin, these spots moreover for the greater part being concealed under the overlapping fore-wing.

VII is totally invisible.

On the under side of the wings the pattern perfectly corresponds with that on the upper side, but on the fore-wing it is paler and partly indistinct, on the hind-wing on the contrary it is sharper and more complete than on the upper surface, because the red hairy covering is absent on the former. The front-rim of the hind-wing, remaining uncovered on this side, sharply contrasts both by colour and pattern with the rest of the wing-surface and wears one especially dark spot, forming the initial component of Bar IV. It seems desirable to indicate this peculiar spot by a special name, as it was also done with those of the fore-wing: viz. the hind-wing-frontborder-spot. In a single of the specimens at my disposal I also found the markings along the front-border of the under side of the fore-wing differentiated and specially spotted.

On the under side of the hind-wing Bar V and VI are not represented, either by their initial (frontal) elements or by other spots of their row, neither can Bar VII be distinguished; the light discoïdal marking however being well visible, as it strongly stands out against the broad anterior part of Bar IV.

Now let us compare this pattern of the Poplar Hawkmoth with that of the Eyed Hawkmoth. The close kinship of *Sm. ocellata* with *populi* appears from several points of correspondence, but surely most convincingly from the possibility of crossing these two species together, the reciprocal hybridisation leading to different results and the hybrids themselves being again fit for propagation. On these accounts the classing of these two species into two different

genera, as proposed by recent systematists, in my opinion does not give a true representation of these relations, but is only a consequence of the immoderate tendency to splitting up, which nowadays is so prevailing in systematic zoology.

To me the comparison between the wing-markings of these two species, so different at first sight, seems highly interesting, especially if the numerous byforms, which are described partly as independent species, partly as subspecies, races, varieties, aberrations etc., are also taken into account. Attention should also be given to the results of hybridisation. But in the first place the under side of the wings should be considered just as accurately as the upper one, and moreover fore- and hind-wing, on both their surfaces, should be compared to each other in detail.

If we do so with *ocellata*, it is easy to see that this species forms one of the innumerable proofs for the assertion, that the difference between fore- and hind-wing, upper and under side, is a consequence of secondary modification of a general primitive pattern, this pattern as a rule remaining better preserved on the under side than on the opposed surface, though as to the latter, the fore-wing usually has retained clearer and more complete vestiges of the primitive pattern than the hind-wing.

Starting with the upper side of this latter, the conviction is easily reached, that the eye-spot, in all its conspicuousness, is yet nothing else but a peculiar modification of parts of three parallel dark bars, each forming the termination of a transverse ribbon (parallel to the wing-border), these ribbons again resulting from the coalescence of a series of internervural spots [1]). Most convincing for this supposition is the comparison of *ocellata* with the nearly related species *Sm. coecus* and *kindermanni*, but it is already rendered highly probable by the comparative inspection of upper and under side of the hind-wing of *ocellata* itself. Such an inspection shows, that on the under side the three ribbons in question are continuous without interruption from behind unto the front border, the outmost one causing near to the hinder angle, where the wing-edge forms an incurvation, a marginal obscuration, which can be retraced on the upper side in the peculiar curved little stem, connecting the eye-spot with the hind border.

On the under side therefore no indication of an eye-spot is present, the dark bars running from before backward without interruption

[1]) This proof has been ably and convincingly delivered by Dr. J. Botke, in his paper: Les motifs primitifs du dessein sur les ailes des Lépidoptères et leur signification phylogénétique. Tijdschr. der Nederl. Dierk. Vereeniging XIV, 1916.

or modification, separated from each other by two narrow, very light intervals.

Along the outer side as well as toward the wing-root these three bars are accompanied by rows of dark spots. The row at the marginal side represents the big semilunar blotch, which occurs on this same place in other species of Smerinthus, and forms the homologue of the corresponding patch at the outer margin of the fore-wing, which occurs in *ocellata* as well as in numerous other species. We here find the convincing proof that this dark marginal area is formed by the coalescence of a row of spots. The middle row of the three ribbons of dark spots is evidently double, its members forming a series of square blocks, whose inner and outer side are formed by dark strokes, sometimes straight, in other cases slightly curved. The outer of these border-strokes are the darkest. The comparison with *populi* proves that these dark strokes represent bar II. As in *populi*, this bar is therefore accompanied at both sides by a dark seam. The one on the outer side is much broader, darker and more independent than the seam on the inner side. The latter is separated from Row III by the inner white band, this row only forming a narrow line, connected by a dark interspace with the very dark and complete Bar IV, which runs along the outer side of the light discoïdal marking, in the same way as in *populi*.

On the under side of the fore-wing the same spots and bars can be found, with the exception of Bar IV, which remains entirely concealed under the wine-red hairy covering of the root-field, just like the posterior part of Bar III. It is only the discoïdal marking, which maintains itself as a small whitish patch in the middle of this reddish covering.

But also on the upper surface of the hind-wing traces of these same bars may be noticed, viz. along the front border, on that part of the wing that remains hidden under the fore-wing during flight, but is protruded in front of it during rest, in consequence of the peculiar attitude of fore- and hind-wing in regard to each other. On this part three dark double-lines run backward up to near the beginning of the red hue, and there end blindly. To my view there is no reasonable ground for the supposition, that these vestiges of pattern should have secondarily crossed over from the fore-wing to the freely protruding part of the hind-wing. On the contrary it seems justified to assume, that they belong to the primary pattern of the hind-wing, as well as their homologues on the under side, or those on the upper side of the hind-wing of *populi*, and have remained untouched by the red discoloration.

Returning to the upper side of the fore-wing, it is at once clear that the same pattern occurs on it as on the corresponding wing of *populi*. It is only somewhat more differentiated: the dark middle area is broken up into a fore- and a hind-part by a narrow funnel-like slit of light colour, along the course of the second cubital vein, while the middle-member of the dark Ribbon II has increased in bulk and shade to a very dark square.

In the same way the anterior and posterior triangular spot, especially the latter, are much more conspicuous and independent than in *populi*.

By proceeding this way we can gradually arrive at the probable conclusion that the patterns on upper and under side of both fore- and hind-wing of *ocellata* repose on one and the same groundplan, and that this primitive pattern has suffered the strongest modification on the upper side of the hind-wing, in consequence of its partial overshadowing by a red discoloration and of the differentiation of the back part of the pattern to an eye-spot.

Should further proof be needed, that the pattern of *ocellata* takes its issue from the same groundplan as that of *populi*, this proof, as already remarked, would be furnished by intermediate forms as *coecus* and *kindermanni*.

As far as the markings on the upper side of the fore-wing, *Sm. coecus* corresponds more to *populi* than to *ocellata*, the transverse bars being more complete and more purely traced than in the latter. Especially the dark middle area is not split up into a fore- and a back-part, the Bars III, IV and V therefore all running straight and unbroken from before backward, V in particular being sharp and dark.

On the hind-wing the eye-spot is less purely circular, because the external (hinder) dark line and the black pupilla-line are less rounded and more advanced toward the hind-margin, thereby giving the impression of fragments of ribbons.

On the other hand the vestiges of original design along the front-margin, hidden under the hind-rim of the fore-wing, are less conspicuous than in *ocellata*.

On the fore-wing of *kindermanni* (Fig. 3) the median area is broken up as in *ocellata*, and in general the similarity with the last named species is greater, the design appearing only somewhat sharper, especially Bar VII looking thereby more conspicuous. The convex blotch along the outer margin is divided into a smaller anterior and a bigger posterior part. The pink hue on the hind-wing is particularly vivid in tone, but the eye-spot is perfectly flat and

composed of three almost similar pieces of dark ribbons, so that its eye-character is almost gone [1]).

On the under side the similarity with *ocellata* is very striking.

By the consideration of the colour-pattern of *ocellata*, as well in itself as in comparison to that of *populi*, we therefore come to the following general statement:

In contrast to *populi*, the pattern on the upper side of *ocellata* deviates from that on the under side, and is moreover composed of two heterogeneous parts, a far-going difference existing between that of fore- and hind-wing. Yet it proves possible to deduce the pattern of both wings from the design of *populi*, which in this latter is especially developed on the upper side, but which can be retraced, be it in a fainter and more reduced condition, on the inferior surface.

The pattern of *populi* therefore satisfies the general conditions of a primitive design, that of *ocellata* those of a secondarily modified, viz.: dissimilarity between the upper side of the fore- and the hind-wing, as well as between the upper and the under side of both wing-pairs, in consequence of deviations of the upper side (of fore- as well as of hind-wings) from the original, simple and regular pattern, but this in a different sense for the two wings, the hind-wing deviating more widely than the fore one. On the first-named a tendency to annihilation of large parts of the pattern by the influence of selfcolour prevails, combined with an extraordinary differentiation of the remaining fragments, this leading to great contrasts between the areas (eye-spot on pink ground). The fore-wing on the other hand shows the complete original design, but transformed over all its components in a more or less similar manner: some parts thereby prevailing above the rest, without affecting however the general harmonious character of the whole.

These facts might easily lead to the conclusion, that the peculiarities in the design of the upper side, by which *ocellata* differs from

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[1]) In parenthesis it may be observed, that we therefore are able to prove for the eye-spot on the wings of the imago a similar origin as A. Weissmann so ably did for those on the body-rings of the larvae of Sphingides, viz. that they spring from fragments of a set of longitudinal, alternately light and dark stripes, these fragments becoming independent and differentiated to concentric circles, while the rest of the stripes disappears totally or nearly so. In caterpillars these stripes run parallel to the body-axis, on the wings of the imagines they are seemingly transverse. Considering wings to be folds of the body-skin, it is easy to conceive, that these so called transverse stripes in reality correspond to longitudinal stripes on the insects' body. Probably the latter stripes may as well as those on the wings be considered as rows of spots which have coalesced together.

1. POPULI

2. OCELLATA

3. KINDERMANNI

4. TILIAE

5. TARTARINOVII

6. LABRUSIAE

E. THEYSSEN, Phot

populi, should be considered as specific features of the first-named form, whereas the points in which the two species resemble each other, especially on the under side, would possess the significance of generic characters. This opinion, that e.g. the eye-spot of *ocellata* cannot pretend to a higher significance than that of being a specific peculiarity, might not only find support in its restriction to the upper side, but also in the results of hybridisation, showing that the hybrids from the cross between a male *ocellata* and a female *populi* are *ocellata*-like in their habitus, though with a faint eye-spot, deprived of its pupilla, whereas those from the combination of a male *populi* with a female *ocellata* possess such a far-going similarity to *populi*, that they can hardly be distinguished from it, the eye-spot being wholly absent.

This view about the meaning of the differential features of *ocellata* seems the more attractive because a special importance for the chances of survival of the animal may be ascribed both to the variegated and marmorated design of the fore-wings and to the eye-spots, in their monochrome pink field, of the hind ones. As long as the moth in its attitude of rest is suspended on a willow-twig among the leaves of that food-plant of its caterpillar, the hind-wings are concealed under the fore-wings with the exception of their narrow fore-rim, and the animal so delusively imitates by its form, colour, design and proportions of a pair of dry willow leaves, that notwithstanding its bulky size it can hardly be detected amongst its natural surroundings, as long as it remains motionless.

When however the sleeping moth gets disturbed by pushing or hurting, it moves its fore-wings a little forward, thereby suddenly displaying the eye-spots in their red surroundings, which by their situation on both sides of the somewhat upheaved abdomen (this part of the body at the same time making periodical jerks) cause the illusion of a savage face with wide-opened eyes, thereby (as experiments have proved) so effectually frightening birds and reptiles, that they generally abstain from further attempts to devour the moth.

When I mention these long known facts from the chapter of Protective Mimicry, it is because I think it desirable to state once more, that they can never be used as an explanation of the presence of markings, hues and shapes, which by their coöperation call forth the deceitful resemblance. These features owe their presence to causes of quite another order of things, viz. to the variability, which itself is a consequence of the coincidence of hereditary factors. When this coincidence accidentally leads to an effect which in a certain direction is favourable for chances of survival of the animal (or plant), it

will always be preserved and ameliorated by the influence of natural selection, so that it will give rise to those highly finished cases of mimicry and protective resemblance which so often raise our astonishment and admiration.

One of the reasons that have made it seem desirable to repeat once more these opinions, however often proclaimed before, is the fact that DE MEYERE in his recent paper "Zur Evolution der Zeichnung bei den Holometabolen Insekten", when arguing on page 59 against BOTKE's views about the wing-pattern of Cossids, declares that he can only see in their design "eine hochgradige Entwicklung einer sympatischen borkenähnlichen Färbung", while on page 48 of his preceding article "Zur Zeichnung des Insekten-, im besonderen des Dipteren- und Lepidopterenflügels", he derives this design "aus einer Zeuzera-pirina-ähnlichen Fleckenzeichnung". To this he adds: "Dieser Weg scheint mir besser verständlich als der umgekehrte". And somewhat further on he says about the transverse markings on the under side of several Vanessidae: "diese scheinen mir mit dem primären Zeichnungsmuster überhaupt nichts zu tun zu haben, sondern es sind eher spät erworbene Elemente der sympathischen Färbung".

The point in these considerations of DE MEYERE which I want to discuss, is not his opposition against BOTKE's views about the connection between spots, stripes and nets, to which I cannot pay full adhesion either, but his assertion, that by considering a wing-design as a "sympathetic pattern" an argument is raised for the explanation of the origin and the discovery of the age of this pattern. Patterns of all kinds, the most original as well as the most strongly modified, may produce a mimicking effect, and thereby prove useful for protective purposes.

E.g. the wing-design of *populi* has quite as much protective value as that of *ocellata*, though only in the sense of resemblance to a weathered poplar-leaf, and yet it is much more primitive than the latter. Moreover the same motives and elements of design, which in one species of animal are the source of highly imitative mimicry, may also be found in other species, near akin as well as far removed in a generic sense, but here, by showing a somewhat different form or by occurring in another part of the body, only cause a feeble sympathetic resemblance or no mimicking effect at all. Of this so called false mimicry EIMER has cited several instances.

Numerous thin, irregular transverse stripes between the veins, in the sense of BOTKE's "traits effilochés", are found except in Vanessidae in many other Lepidoptera of diverse families: also in Sphingides,

on both wing-sides, though most frequently on the under side. In a general survey of the wing-markings of Lepidoptera, which I undertook long before Botke's doctor-dissertation, and wrote in English, but which I did not hitherto publish, I even thought it desirable to choose a special name for this curious motive of design and called it "Cosside markings".

Now it might very well be, that these markings could also be reduced to an old and original motive of design, occurring generally among insects, and whose connection with the system of internervural spots still wants elucidating, although Botke has made a notable attempt to come to a general theory.

That a "sympathetic" design, on account of its mimetic character, should necessarily be younger than other patterns, I deny most emphatically. Each of the elements, which by their coöperation produce the mimetic effect, may in itself depend on hereditary tendencies of very high phylogenetic antiquity. Only the specific and special culmination of that coöperation may be young, and even this need not necessarily be the case. Among Pierids, Papilionids and Nymphalids the mimicrists probably often wear an older and more primitive uniform than the remaining so-called typical members of these families, as I have tried to demonstrate in my paper read at the International Entomological Congress at Oxford in 1912.

In numerous Geometrids, issuing from their pupae in autumn, the similarity to a weathered leaf reposes on their light-yellow colour, besides on the broken rim of their wings and the course and arrangement of dark transverse lines on them, imitating the veins of the leaf. Must on this ground the yellow hue be younger than other tints? According to my view this need no more be the case than it need be assumed for the form of the wing-border or the pattern on its surface, even when granting that in general a broken border-line has to be derived from an unbroken, rounded one.

In the same way the evident connection between spots, stripes and meshes on the wings of Cossids, which can so to say be read on the wing-surface by simple observation and by comparison with the Zeuzerids, is in no way brought nearer to an explanation by the remark, that the preponderance of the net-markings produces a sympathetic resemblance to the bark of trees. The real question remains: what causes tendency of the Cossid wing-markings to the net-character and how old is that tendency? In putting this question we have to keep in view, that the same tendency occurs in many other insects

belonging to different orders and that it may likewise be remarked in the nervural system, which possesses such intimate and primordial relations to the distribution of pigments in the skin.

Were it only to consider this question from all possible points of view, the well-foundedness of the hypothesis would have to be tried, whether net-design may be connected with the formation of meshes in the system of wing-nervures, as is so frequently and specifically found in Neuroptera and Orthoptera, vicariating with regular transverse venation; whether therefore the net-design may not be as old as or even older than spots or stripes. An argument to this assertion might be found in the fact, that nets between the longitudinal veins are characteristic of the nervation of the wings in Palaeozoïc Palaeodictyoptera.

With this inference I do not in the least intend to proclaim, that I am convinced of this connection of the net-design and of its phylogenetic antiquity, but simply that I think the contrary is not proved either.

Remembering Weismann's words: "Ohne Hypothese und Theorie giebt es keine Naturforschung", I am of opinion that the continual proposing of explaining suppositions about the connection between corresponding phenomena is necessary condition for fertile scientific research, and therefore I cannot adhere to de Meyere's point of view, where he says: "Ich möchte mich, den Tatsachen entsprechend, mit Feststellung des Auftretens begnügen und keine ganz hypothetische Verbindungslinien ziehen."

Returning to the specific differential characters of *Sm. ocellata*, I here find the danger to get entangled in purely hypothetical speculations not by any means serious. For it can be easily proved that all the special characteristics of the upper side of both fore- and hind-wings occur as well in other species, not only of the genus Smerinthus, but also of different allied genera.

In the first place the comparison with *tiliae* is highly instructive. On the upper side of the fore-wing of the Limetree-Hawkmoth every peculiarity by which the pattern of *ocellata* deviates from that of *populi*, is again met with, but in a modified form and in other hues, which together produce a totally different effect of the wing-design as a whole.

Especially striking is the similarity of the dark median area with the same wing-part of *ocellata*; as in the latter it is cut up into a fore- and a hind-quarter by funnel-shaped intrudings of the light-brown ground colour, which may either meet each other or remain separate. A single look at every somewhat considerable collection

of *tiliae* shows the extreme individual variability of this feature, as well as of others. The transition of an unbroken middle-field to one divided into an anterior and a posterior portion we therefore here see take place under our eyes.

We may likewise notice, that the peculiarity of the central (5th) mark of the dark Bandline II, to differ in hue and size from the other members of that series, is also present in *tiliae*, but in so far in an opposed sense, that in some specimens it is distinguished by a lighter instead of a darker shade. On its underside, *tiliae* shows again the same simplified pattern as *populi* and *ocellata*, viz. the two Bandlines II and III, with traces of I, IV and VI.

The right here to speak of simplification, and to connect this with the covering of light hairs stretching from the wing-root outward as far as the middle area, is strikingly proved in this case by the vestiges of the opaque central blotch (so strongly developed on the upper side) which can also be detected on the under side. At the root of each hair in the area of this dark middle-field a small black speck may be perceived, and this produces the effect that the field is seen in its full extension as a collection of specks, when we look obliquely between the hairs.

Still more striking than the resemblance between *tiliae* and *ocellata* is that between both these species and *tartarinovii*, this latter offering so to say a form of transition between the first-named two. Here the anterior part of the external margin of the opaque middle area is not convex as in *tiliae*, but is concave, while a contrast both in hue and in markings exists between the anal field of the wing and the rest of its surface, the division of the central field in a fore- and a hind-part thereby appearing as part of a process which extends over the whole length of the wing-surface, in the same way as in so many other Lepidoptera and even in Insects of other orders.

It is likewise remarkable, that the apex of the fore-wing, which shows a special differentiation identical for all these species, viz. that it is separated from the remaining markings by the oblique light stria already described for *populi*, is dark greenish grey instead of silvery grey, in contrast with the convex blotch along the outer margin, which is stained in light grey, while it is dark in others.

On the hind-wing *tartarinovii* displays the same pink as *ocellata*, and even traces of an eye-spot.

On the other hand in *tiliae* a dark band extends over the entire surface of the hind-wing parallel to the outer margin and at some distance from it. This band evidently consists of as many components

as there are internervural cells. Each component is prolonged wedge-like in the direction of the wing-root. The extent of this prolongation is individually different, though in general it may be stated, that in a backward direction toward the hinder wing-edge the dark internervural spots get larger and more intensively black, this backward increase in size and darkness being the only indication of a similarity to the eye-spot of *ocellata*.

Therefore, though in this latter instance *tiliae* shows almost as little likeness to *ocellata* as does *populi*, this does not derogate from the truth and the value of the fact, that in numerous Sphingides the hinder external angle of fore- as well as of hind-wing shows a dark pigmentation, which may be differentiated to an eye-spot. This might also be expressed otherwise, by saying that the above-mentioned posterior triangular spot is not restricted to the fore-wing, but returns on the hind-wing.

And also on the fore-wing the spot in question may assume the character of an eye-spot, as is shown by several Sphingides belonging to different genera, e.g. *Daphnusa ailantha*.

On the other hand, as already said, other species possess near to this hinder external angle of the fore-wing only a single or double, solid blotch not differentiated to an eye-spot, e.g. *Oxyambulyx canescens*. Also this blotch may be repeated on the hind-wing, e.g. *Smerinthus quercus*.

Among the Sphingides at my disposal *Pholas labrusiae* (Fig. 6) seems to me to possess a highly remarkable colour-pattern. On its under side the similarity between fore- and hind-wing is very great, and both show the usual simple design of Lines II and III on a nearly homogeneous faint greenish-yellow ground, to which only along the external margin a differently coloured area, separated from the rest of the wing-field by a zigzag line, and evidently representing Bar I, is added. But on the upper surface the contrast between the two wing-pairs is very profound. The fore-wings are almost unicolourous dark opaque green, exactly corresponding in hue to the entire body of the moth. Yet several traces of dark transverse lines are well defined, especially the middle-field between Bars III and IV, which is conspicuous by a somewhat darker green shade. But at the external border of this middle-field two square little areas are so to say spared out from the general green overshading: one nearly in the centre, the other at the back margin, thereby giving the impression of brown curtains before two low windows in a green wall. That impression is strengthened by the fact, that in these brown areas the curved components of the transverse dark bars are more numerous

and far sharper than in the green field. In the central window 4 of these arched stripes are present, in the back one 2.

Comparison with *Smerinthus populi* and *ocellata* as well as so many other Sphingides, whose ground-colour is brown or grey, and whose transverse bands are composed of curved, stripy spots, leads to the supposition that in these windows we have to see remnants of the original hue and design of the wing, which for the rest has become indistinct by green discoloration.

As in so many other cases, e. g. the Hepialids, green therefore would be the secondary, brown the primary hue, the design having partly get lost in the process of discoloration or at least having greatly diminished in distinctness. But why these two brown windows with their trelliswork of curved stripy spots have remained untouched by this process, I cannot as yet explain.

Contrasting with the almost homogeneous green hue of the fore-wing, the hind one possesses a very showy and variegated pattern: two jetblack bars standing out against a light yellow ground, bluish-grey areas occurring at the front border between the black, a brickred patch vicariating with two black strokes near the inner margin, while at the outer one a small green field breaks the yellow.

But the most remarkable point in this pattern are two darkbrown, irregular, denticulate lines, starting at the hinder angle, and running parallel to the outer margin along its posterior part, to pass into the broad black bar at the hinder border of the small green field. These crooked lines represent the posterior part and the pupilla of the eye-spot in the *ocellata*-group among Smerinthidae, and form the least-modified part of the hind-wing-pattern of *Pholus labrusiae*.

I think it highly probable, that this pattern has a protective significance for the animal, just as well as the almost homogeneous green hue of the fore-wings and of the body. The latter give protection to the sleeping animal by making it hardly visible to enemies that prey upon it, possibly the brown windows play their part in this process of concealment, by breaking the anatomical lines of the rather extensive wingfield.

It certainly would be worth while to make the experiment, whether the moth when disturbed in its sleep, suddenly displays its hind-wings and so frightens its enemies away, or whether the showy colour-composition, which thereby gets visible, has only the meaning of a warning-pattern, announcing unpalatableness.

Whatever may be the right interpretation, this pattern in any case ought to be considered as a high and special differentiation of the original one of the hind-wings, common to all Sphingides; neither

the crying colours nor their queer arrangement justifying the inference that they could ever be the direct consequences of the useful effect they produce in favour of the animal.

The comparison of *Sm. ocellata* with *populi*, and of both with other Sphingides, leads me to the following conclusions:

The colour-pattern of *populi* is more primitive than that of *ocellata*, it agrees with the conditions which may be posed for a primordial pattern, and it corresponds to the fundamental plan, as this is found in Arctiïds, and most probably in numerous other families of Heterocera, possibly also in Rhopalocera. It therefore is not only older than the genus Smerinthus, but even than the family of Sphingides, perhaps than the entire order of Lepidoptera. So it cannot without great restriction be qualified as a generic pattern.

The colour-design on the upper side of *ocellata* can be derived from that of *populi* by the assumption, that the ribbons of internervural spots occurring in the latter have been specially transformed in the former. But each of these transformations in itself is seen as well in other species of Smerinthus, and even in many other genera of Sphingides, it is therefore not allowable to assume, that they should have been acquired during the formation of *ocellata* from a *populi*-like ancestor. Each for itself they are not characteristic of *ocellata*, and cannot be taken as specific features of this species. It is only the peculiar combination of the modifications of the ancestral type with the subtle nuances by which in *ocellata* they are distinguished from the similar modifications in allied forms, that in the end give the specific character to *ocellata*. At any rate the origin of the said modifications of the primitive pattern cannot be ascribed to the influence of protection against enemies, which *ocellata* obtains by the use she (instinctively) makes of her eye-spots. The special refinement however and the elaborate details, by which the pattern of *ocellata* surpasses that of other Sphingides near akin, may well be the consequence of natural selection, which could enter into action as soon as by coïncidence of hereditary variations of the fundamental Sphingidial pattern with special circumstances of life, a deceitful likeness had been established to the face of a big-eyed owl, which frightened away preying little birds and small mammals.

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